

# NON-AUTOSTYLIC PENNSYLVANIAN INIOPTERYGIAN FISHES

by BARBARA J. STAHL

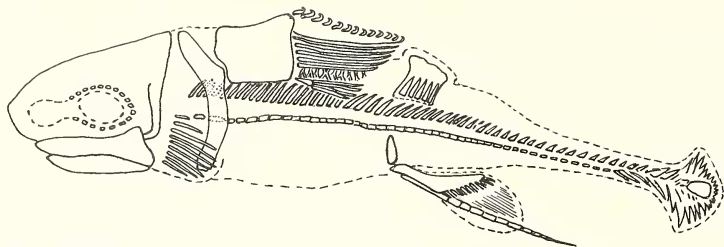
**ABSTRACT.** Further study of iniopterygian fishes from the Pennsylvanian of North America has shown that autostylic jaw suspension is not, as was originally thought, a characteristic of the group. Two of the five genera possess palatoquadrate elements that articulate with the neurocranium, a fact that calls for modification of the history of the mandibular arch tentatively proposed for these fishes.

No problem has proved more puzzling to students of lower vertebrates than the evolution of the Palaeozoic chondrichthyan fishes. Studies of Recent forms show the association of elasmobranchs and holocephalians in the class Chondrichthyes, but within that category much remains to be clarified, particularly concerning the interrelationships of the oldest forms. Until recently, holocephalians could be traced through the fossil record only to the Jurassic. Association of earlier forms with this group was highly speculative. In the case of the elasmobranchs, Palaeozoic representatives have long been known, but they are variously specialized, and the nature of their relationship is not evident. The origin of all these cartilaginous fishes is rooted in or near the extinct Placodermi. Moy-Thomas and Miles (1971) regarded the chondrichthyans as diverging from placoderms and then differentiating into elasmobranchs and holocephalians. Others suggested the evolution of elasmobranchs and holocephalians from separate placoderm ancestors (Örvig 1960; Stahl 1967).

During the last twenty-five years a significant number of chondrichthyan fishes has been recorded from sediments of Carboniferous age in the American mid-continent. Proof that broad diversification of this group existed in the shallow marine and brackish waters that covered the area extending from Indiana west to Kansas and Nebraska, and northward into Montana, indicates that in earlier Palaeozoic times a radiation of chondrichthyans—perhaps geographically very broad—had taken place, of which palaeontologists were barely aware. Zangerl (1973) lists six groups of elasmobranchs on the basis of distinctive body design, and Zangerl and Case (1973) describe a new order of chondrichthyan fishes, the Iniopterygia, whose relationships have yet to be defined. If, however, the newly discovered fossils complicate the history of the class Chondrichthyes, they also provide more evidence to elucidate it.

The discovery of the Iniopterygia is regarded as particularly interesting because the fishes in this group share derived characters with the chimaeroid holocephalians, and may thus reveal something about the affinities of the latter group. Although the iniopterygians show structural similarities to both elasmobranchs and chimaeroids, they are surely not phylogenetic intermediates. Their own structural specializations—notably the dorsally placed articulation of the pectoral fin basals on the pectoral girdle—make that idea implausible.

Zangerl and Case reconstructed the iniopterygian fishes as being chimaeroid in body-form: stout anteriorly with the reduced caudal musculature characteristic of leisurely swimmers (text-figs. 1 and 2). They thought that the fishes propelled themselves to some extent with wing-like movements of the broad pectoral fins. The skull of the iniopterygians was relatively short, with the gill arches crowded forward under an operculum stiffened by cartilaginous rays attached to the hyoid elements. Like elasmobranchs, their teeth were separate (at least at the cusps) and organized in tooth families. They had, as did the Palaeozoic sharks, long radial cartilages in the pectoral and caudal fins, and a long-jawed terminal mouth.



TEXT-FIG. 1. *Iniopteryx rushlaui*. Reconstruction of skeleton and outline of body. Modified from Zangerl and Case.

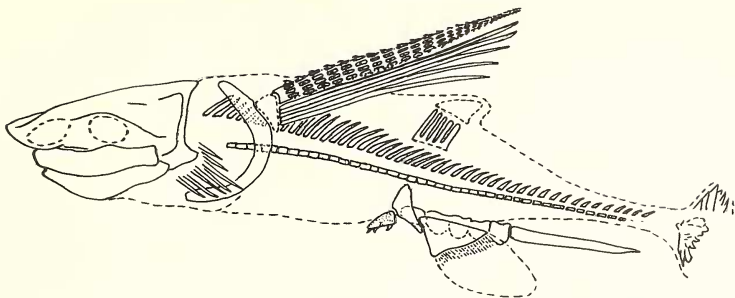
Zangerl and Case stated initially that the palatoquadrate cartilages were fused to the neurocranium in iniopterygians as they are in chimaeroid holocephalians. Classifying these two kinds of fishes in sister-groups—the orders Iniopterygia and Chimaerida of the subclass Holocephali of the class Chondrichthyes—the senior author supposed autostyly to be a shared, derived (synapomorphic) character that distinguished holocephalian from elasmobranch chondrichthyans.

The discovery that autostyly is not characteristic of all the iniopterygians has implications not only for the history of these fishes but also for the origin of the chimaeroids.

#### MATERIAL AND METHODS

The iniopterygians whose jaw suspension is described here as being non-autostylic are *Iniopteryx rushlaui* and *Promexyle peyeri*, forms placed in the family Iniopterygidae. They are known from the Wea Shale and the Stark Shale, upper Westphalian D (*Iniopteryx*) and the Labette Black, Excello, Mecca Quarry, and Logan Quarry Shales, lower Westphalian D and C (*Promexyle*) of the Pennsylvanian. The new specimens discussed in this paper were obtained from the Mecca Quarry Shale at Hesler quarry, Parke County, Indiana, and were collected by a Field Museum of Natural History (FMNH) party in 1973. At this site both *Iniopteryx* and *Promexyle* are relatively common. Only those specimens with the most favourable preservation of the braincase and/or branchial elements were studied: *I. rushlaui*: PF 3098, PF 8560, PF 8561, PF 8562, PF 6661, PF 6677; *P. peyeri*: PF 8563, PF 8564, PF 8565, PF 8026, PF 8566, PF 2358, all in the collection of the Field Museum of Natural History, Chicago.

Since the specimens, composed of calcified cartilage, are wholly covered by the shale in which they are embedded and cannot be exposed by removing the matrix, they were studied in stereoscopic X-rays prepared by the method described by Zangerl (1966). The use of the stereoscopic technique makes it possible to reconstruct the three-dimensional form of the braincase and to differentiate branchial elements that are superimposed in the shale. Interpretation of the fossils is complicated by the fragmented or twisted state of some of the branchial elements and by a reduction in the depth of those braincases preserved with their dorsal and ventral surfaces parallel to the bedding plane of the shale. Deformation of the braincases is not extreme, because it resulted from the slight settling of the mineralized material of the skeleton, in loose, undisturbed sediment, as the organic cartilaginous framework holding the crystals gradually decayed. Subsequently little or no compression took place. Since a braincase of *Iniopteryx* preserved in lateral orientation was available (text-fig. 3), the vertical dimension of the skull in that form could be reconstructed with a relatively high degree of confidence. The accuracy of the form of the branchial elements used in the reconstructions was checked, where possible, by comparing homologous elements in two or more specimens.

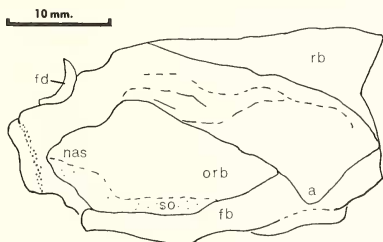


TEXT-FIG. 2. *Promexyele peyeri*. Reconstruction of skeleton and outline of body. Modified from Zangerl and Case.

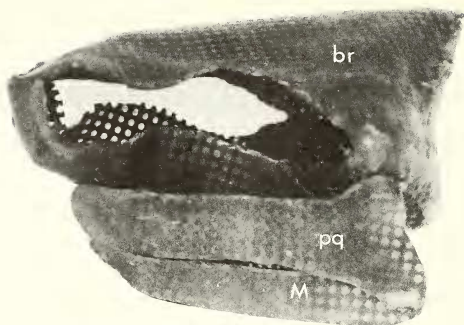
To verify the anatomical relationships visualized from the X-rays, three-dimensional models of *Iniopteryx* and *Promexyele* were made (text-figs. 4 and 5). Association in the shale of the braincase and branchial elements supports this reconstruction which produces a head skeleton that could have fulfilled the functions it served in life.

#### OBSERVATIONS

In both *Iniopteryx* and *Promexyele* the braincase lacks the pair of densely mineralized facettes that is present on the ventral surface beneath the posterior margin of the orbits in *Iniopera* and *Sibyrhynchus* (the braincase of *Inioxeyele* is not known well enough to make description of this area possible). These facettes, which faced anteriorly from robust ventrolateral protrusions of the braincase in the latter two genera, were identified by Zangerl and Case as points of articulation of the lower jaw. In the absence of these abutments for Meckel's cartilages, the neurocrania of *Iniopteryx* and *Promexyele* appear more similar to the braincases of contemporary sharks than to those of chimaeroid



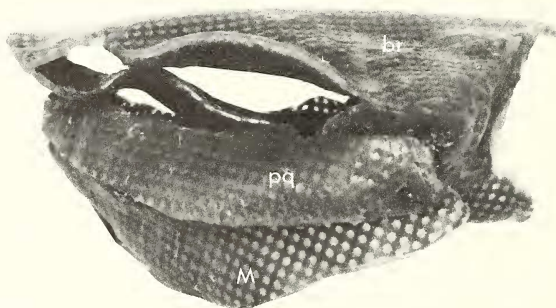
TEXT-FIG. 3. *Iniopteryx rushlaui*. FMNH PF 8560. Lateral view of braincase. Drawn from radiograph. a, area of articulation for palatoquadrate; fb, floor of braincase; fd, displaced fin ray denticle; nas, nasal cavity; orb, orbit; rb, roof of braincase; so, suborbital shelf.



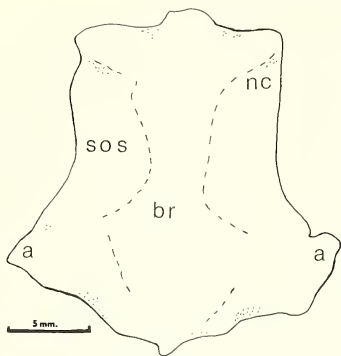
TEXT-FIG. 4. *Iniapteryx rushlaui*. Model of braincase and mandibular arch in lateral view. br, braincase; M, Meckel's cartilage; pq, palatoquadrate.

holocephalians. In both genera, the posterior part of the braincase is short: in *Iniapteryx* (text-fig. 6) the region posterior to the orbit is about a third, and in *Promexyle* (text-fig. 7) slightly more than a third, of the length of the skull. In each, the supraorbital shelf continues posteriorly into a postorbital process that curves ventrad and bears at its terminus a surface that is shaped as if it were a point of articulation. This projection is supported from below by a densely mineralized strut that extends dorsolaterally from the floor of the braincase behind the orbit.

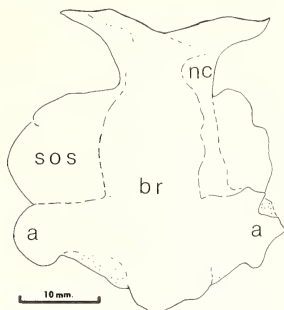
Although the end of the postorbital process is not reinforced by as dense a layer of mineral crystals as exists on the facettes for the lower jaw in *Iniopera* and *Sibirhynchus*, it still seems likely that it was the point of attachment for a jaw element. The surface bears a shallow groove in which an opposing cartilage could have ridden fore and aft, and the postorbital process, with its ventrally supporting



TEXT-FIG. 5. *Promexyle peyeri*. Model of braincase and mandibular arch in lateral view. br, braincase; M, Meckel's cartilage; pq, palatoquadrate.



TEXT-FIG. 6. *Iniopteryx rushloui*. FMNH PF 3098. Braincase in dorsal view. Drawn from enlarged radiograph. a, area of articulation for palatoquadrate; br, braincase; nc, nasal capsule; sos, supraorbital shelf.



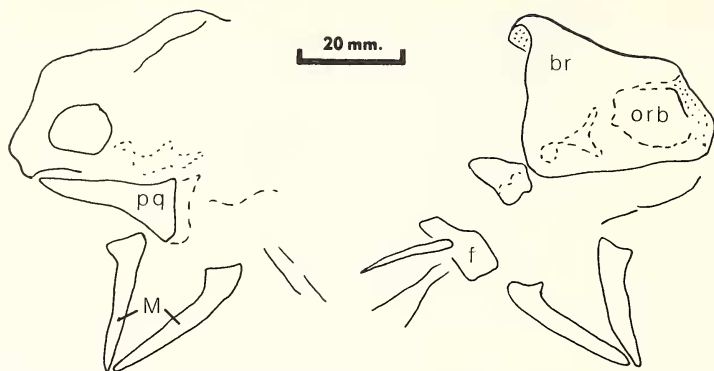
TEXT-FIG. 7. *Promexyle peyeri*. FMNH PF 8563. Braincase in dorsal view. Drawn from enlarged stereoradiographs. a, area of articulation for palatoquadrate; br, braincase; nc, nasal capsule; sos, supraorbital shelf.

strut, forms a mechanical arch through which stress would have been projected dorsally and ventrally against the more central part of the braincase.

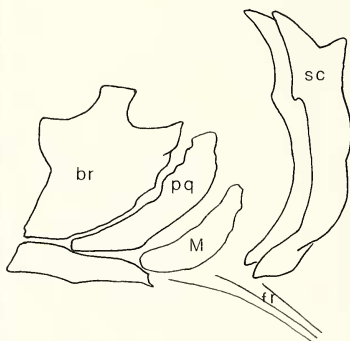
In both *Iniopteryx* and *Promexyle*, the ventral surface of the braincase narrows anterior to the struts that extend to support the postorbital articular processes. The resulting space left ventral to the orbit and posterior to the laterally flaring nasal capsule accommodates the greater part of the palatoquadrate when that element is placed in articulation with the end of the postorbital projection. No anterior articulating process is clearly evident on any of the palatoquadrate cartilages through which a second abutment against the braincase could have been made, but the tip of the palatoquadrate fits snugly against the neurocranium ventral to the nasal capsule, allowing the possibility of a ligamentous tie in that area for greater stability.

The form of the palatoquadrate and mandibular elements in both *Iniopteryx* and *Promexyle* is similar to the basic structure of epibranchial and ceratobranchial arch elements. Whether their lack of greater specialization is primitive or secondary cannot be decided on the evidence available. The palatoquadrate, rather than possessing the broadly expanded posterior end with the otic process characteristic of sharks, is much more uniform in width along its length. In *Iniopteryx*, the palatoquadrate can be identified in only two specimens, PF6677 (text-fig. 8) and PF6661. In both, the element is only slightly flared posteriorly, where it articulates with the braincase dorsally and the mandible ventrally. The body of the palatoquadrate is a little broader than that of the lower jaw and tapers at the anterior end. The palatoquadrate of *Promexyle* is even more bar-like (text-fig. 9A), neither widening posteriorly nor tapering at the front. The element has been observed in all the specimens of *Promexyle* examined by the author and has been identified in at least nine others by Zangerl (pers. comm.).

In contrast to the palatoquadrate of *Iniopteryx*, the mandibular elements are clearly seen in numerous specimens. They bear a short, pyramidal process which projects dorsad immediately anterior to the articular facette at the posterior end. The body of the element is straight and narrows to a point anteriorly. Although still relatively simple in design, the mandibles of *Promexyle* are quite different from those of *Iniopteryx*. In *Promexyle* the lower jaw is bar-like at the rear, but anteriorly



TEXT-FIG. 8. *Iniapteryx rushlaui*. FMNH PF 6677. Braincase with palatoquadrate in place and Meckel's cartilages preserved below. Drawn from the fossil directly. Plate at left; counterplate at right. Note superimposition of palatoquadrate cartilages visible on plate. br, braincase; f, fin elements; M, Meckel's cartilage; orb, orbit; pq, palatoquadrate.



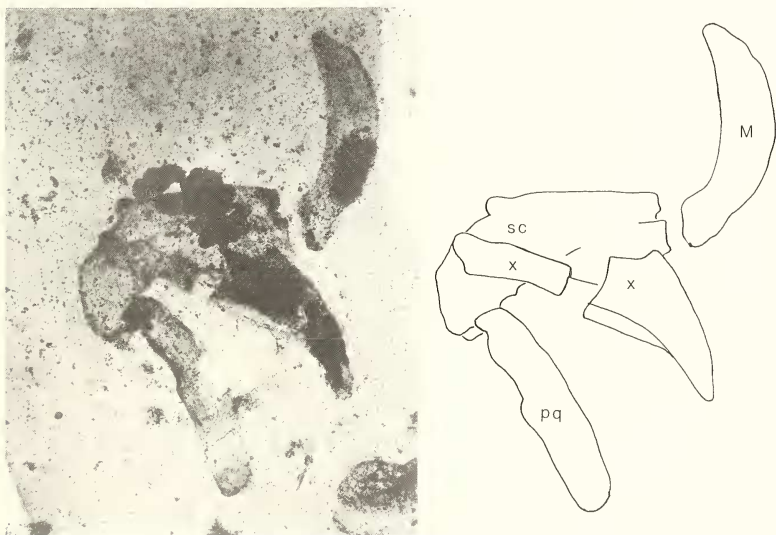
TEXT-FIG. 9A. *Promexyle peyeri*. FMNH PF 2358. Skull and pectoral girdle in lateral view with jaw elements approximately in place. Radiograph  $\times 1$ . Explanatory sketch alongside. br, braincase; fr, fin rays; M, Meckel's cartilage; pq, palatoquadrate; sc, scapulocoracoid.



one edge is straight and the other broadly curved (text-fig. 9B). Frequently, a row of tooth-wells can be seen parallel to the long axis of the element in its broadest portion.

In life, neither the palatoquadrate nor Meckel's cartilage was fused to its counterpart on the opposite side. Since the elements of the mandibular arch in *Iniopteryx* and *Promexylele* have never been found united with their opposite members (unlike the Meckel's cartilages in *Iniopera* and *Sibyrhynchus*), the upper and lower jaw cartilages are assumed to have been bound by ligaments to those of the other side, or perhaps, in the case of the lower jaw, to have abutted a small median cartilage which has gone unrecognized in the specimens studied.

The branchial skeleton posterior to the first arch is composed of more delicate elements that are fragmented in the available specimens, and generally preserved inextricably jumbled in a narrow plane. It is therefore not possible to describe with certainty the structure of the hyoid arch or its exact spatial relationship to the jaws. The presence of what appears to be a small, curved flange on the rear of the braincase posterodorsal to the articular surface for the palatoquadrate may well have been the point of attachment for the epihyal cartilage. The flange is suggested, rather than clearly preserved on some of the braincases, so only the most tentative suppositions should be based upon it. Observations suggest that the articular surface rimmed by the small flange faced posteriorly. If this were the case, the epihyal would probably have extended posteriorly, and therefore may not have come in contact with the jaw-joint to support it.



TEXT-FIG. 9B. *Promexylele peyeri*. FMNH PF 8563. Jaw elements disarticulated and displaced. Radiograph  $\times 2$ . Explanatory sketch alongside. M, Meckel's cartilage; pq, palatoquadrate; sc, scapulocoracoid; x, unidentified elements.

## DISCUSSION

The existence of iniopterygian fishes with autostylic and non-autostylic jaw suspension raises numerous questions concerning the adaptation and phylogenetic history of the group. Palaeontologists generally seek to distinguish the geographical range and the particular habitat of the animals in question and then to link the acquisition of specialized structures to the niches and natural selective forces that they have defined. As a general rule, they discover some correlation between the animals' feeding habits and mode of locomotion expressed in co-ordinated structural modifications. The iniopterygian fishes present a paradox: although jaw suspension within the group differs in a way that is functionally significant, they were essentially sympatric and appear to have shared the same environment. The deposition of their remains in similar shales in the shallows edging the Pennsylvanian epicontinental sea demonstrates their common exposure to a peculiar and restrictive set of conditions described by Zangerl and Richardson (1963). They believe that in these waters, there was no bottom-dwelling fauna because of toxic compounds from anaerobic decomposition that occurred in the dense, quiet mud. Therefore, unable to live like holocephalians on hard-shelled molluscs and other bottom-living invertebrates the autostylic iniopterygians, like their non-autostylic relatives, would have been confined to the mass of water-weed that floated above the mud. Doubtless, the smaller animals in the weeds together with the plant material would have sustained the slow-swimming iniopterygians. The palaeohabitat in which the iniopterygians have been discovered offers no evidence to elucidate the circumstances which favoured, in the same order, the retention of an identical body-form (and hence the same locomotor style) and the development of both autostylic and non-autostylic jaw suspension, arrangements that imply different diets. Further insight awaits the finding of these forms in other locations where environmental conditions were less transient and offered a greater variety of niches.

The presence of non-autostylic iniopterygians poses a problem for modern taxonomists whose classification schemes are intended to reflect evolutionary relationships. In their view, the autostyly of the extant chimaerids is one of the chief traits that separates these fishes from elasmobranchs. In regarding jaw suspension as a key character, current workers are following a practice that has influenced the interpretation of piscine relationships for many years. Huxley (1876) used autostyly to distinguish lungfishes from bony fishes in which the hyomandibular gave support to the jaws. Gregory (1904), arguing that the autostyly of chimaerids was different from that which appeared in lungfishes, called the chimaerid form of jaw suspension holostyly. The fusion of the palatoquadrate with the braincase led to the name Holocephali for the taxon housing the chimaerids, and Patterson's (1965) attempt to classify a wide variety of bradyodont chondrichthyans as holocephalians was resisted by Zangerl and Case and by Lund (1977a), because there were non-autostylic forms among those fishes. Zangerl included the Iniopterygia within the Holocephali because, in addition to the opercular flap and general body-form, the members of the group seemed to have had the upper jaw fused to the neurocranium. His description of the Iniopterygia and the Chimaerida as sister-groups implied the evolution of holostyly in a common ancestor, presumably a divergent elasmobranch that formed the root of the holocephalian line. The description by Lund (1977b) of a chimaeriform fish from the late Mississippian Bear Gulch limestone of Montana favoured Zangerl's evolutionary hypothesis.

Unless the non-autostyly of *Iniopteryx* and *Promexyle* is secondary, which seems unlikely, it must now be assumed that the common ancestor of the iniopterygians and the chimaerids had a palatoquadrate suspended in shark-like fashion. The first holocephalians would not have merited the name, and autostyly or holostyly would have evolved in fishes of this group at least twice. Positing the independent and parallel evolution of an autostylic palatoquadrate within the Holocephali is not of great help in determining the origin of the group, but it does tie the holocephalians more closely to the elasmobranchs and makes alliance with any other forms remote. One may speculate, as the classification scheme of Arambourg and Bertin (1958) implies, that the holocephalian fishes expressed in the most extreme form the tendency among a number of early Palaeozoic chondrichthyans to develop fusions of teeth, jaws, and neurocranium. In other lines that took this evolutionary



course, grouped by Arambourg and Bertin as Eubradyodonti, tooth whorls or tooth plates appeared, but autostyly was rarely if ever reached.

If the non-autostylic iniopterygians were archaic in retaining a jaw suspension resembling that of their ancestors, it is reasonable to look to them for clues to the primitive condition of the mandibular and hyoid arches. Besides the discrete and unspecialized form of the jaw elements, the most striking characteristic of the first arch is the relative fragility of the palatoquadrate. In *Iniopteryx*, which had rows of very small conical teeth, suggestive of a weak bite, the upper jaw cartilage, unlike the mandibular element, is not generally preserved without breakage or deformation. In neither *Iniopteryx* nor *Promexyle* does the palatoquadrate present broad or tall projections that would have afforded an area of attachment for strong ligaments tying the upper jaw to the neurocranium. The palatoquadrate in these iniopterygians is thus unlike the homologous element in the Pennsylvanian sharks *Cobelodus*, *Dentaea*, and *Symmorium*, that Zangerl and Williams (1975) regard as primitive. In these elasmobranchs, the palatoquadrate, possibly not supported by the epihyal element of the second arch, is expanded posteriorly and braced firmly against the braincase through three abutments. In the opinion of Zangerl and Williams this rigid attachment of the palatoquadrate gave way to arrangements that provided greater freedom of movement in more advanced elasmobranchs. If that hypothesis is correct, and the design, primitive for sharks, is also primitive for gnathostomes, the structure and style of attachment of the upper jaw in the non-autostylic iniopterygians would have to be considered secondary rather than reflective of an early stage in the transformation of a branchial arch into jaws.

Evidence concerning the structure of the hyoid arch is insufficient to support speculations about its suspensory function. Logic suggests, and Watson (1937) and Zangerl and Williams state, that the earliest gnathostomes probably had an unspecialized hyoid arch separated far enough from the mandibular arch to allow a full gill slit between them; a condition described by Watson as apthetohyoidean. If the Pennsylvanian elasmobranchs analysed by Zangerl and Williams were in fact apthetohyoidean, and if the condition were to be found in the Iniopterygia, the possibility that apthetohyoidy was present in the earliest gnathostomes would be enhanced. Available fossil material provides for *Iniopteryx* and *Promexyle*, no regularly identifiable complete hyoid arch elements that would give certainty to a reconstruction. The orientation of the facette on the braincase that apparently provides an abutment for the epihyal suggests, besides the absence of a pharyngohyal, that the epihyal was directed posteriorly; an arrangement that would have left a space between the first and second arches. However, the possibility that that space would have contained a gill slit seems diminished by the operculate character of the iniopterygian fishes. In extant operculate forms (both in the chimaerids and bony fishes), the gill arches are crowded and set forward under the rear of the braincase. As a result, the prehyal slit is never present except as a spiracle, and is usually obliterated altogether. Since the delicacy of the branchial arch elements apparent in the iniopterygians suggests a similar reduction and crowding in the gill region, it seems more probable to speculate against apthetohyoidy in these fishes.

## CONCLUSION

The discovery that the palatoquadrate cartilage is not fused to the neurocranium in *Iniopteryx* and *Promexyle* requires the removal of autostyly as a characteristic of the family to which these genera belong. The taxonomist is thus left with fishes within the sub-class Holocephali that are surely quite closely related to other holocephalians and yet lack a diagnostic feature of the group. Implications relating to the phylogeny of the holocephalians are also apparent: the source of the line was most likely not a population of sharks that had evolved fusion of the upper jaw and braincase, but one that possessed the genetic potential for doing so. Presumably, as the stock diversified, autostyly evolved in parallel. In their jaw suspension, *Iniopteryx* and *Promexyle* would have been archaic forms.

Whether these iniopterygians retained traces of the arrangement of the first two branchial arches that was primitive for chondrichthyans or gnathostomes generally, is less clear. Resolving this

question, as well as understanding the selective forces that produced functionally very different jaws in iniopterygians of similar body-form, will be possible only if earlier Carboniferous and Devonian cartilaginous fishes are found.

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